# VARIATION IN THE CRANIAL OSTEOLOGY OF THE AUSTRALO-PAPUAN HYLID FROG *LITORIA INFRAFRENATA*

by

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## *ABSTRACT*

DAVIES, M. 1977. Variation in the cranial osteology of the Australo-Papuan hylid frog *Litoria infrafrenata*. *Rec. S. Aust. Mus.* 17 (22): 337-345.

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The cranial osteology of specimens of *Litoria infrafrenata infrafrenata* from Tully (Queensland) and Aitape (New Guinea) and of *Litoria infrafrenata militaria* from Keravat (New Britain) were examined. The species were chosen because of their wide geographic range and known isolation for a considerable period of time, with a view to establishing the validity of skull character states as good species indicators. The only noteworthy variation found was in the extent and degree of ossification; the extent of development of the sphenethmoid in relation to the nasals; the relationship of the otic ramus of the squamosal to the crista parotica; the extent of development of the zygomatic ramus of the squamosal; and the shape and nature of the dentigerous processes of the prevomers. Examination of these characters only distinguishes those populations recognised already as subspecies. In view of the extent of isolation of Australia and New Guinea it is concluded that the character states examined are valid species indicators.

## INTRODUCTION

Studies are currently in progress in this laboratory on the hylid frogs of the genus *Litoria* of Australia and New Guinea to establish species groups in *Litoria*. Three major lines of investigation—myology, karyology and osteology—form the basis of the study.

Little has been published to date on the cranial osteology of the Australian hylids. W. K. Parker (1881) described the skulls of *Litoria caerulea*, *L. phyllochroa*[1], *L. ewingi* and *L. bicolor*, Keferstein (1868) described the skull of *L. aurea* and *L. freycineti* whilst Gillies and Perbody (1917) described the skull of *L. caerulea* with some references to that of *L. aurea*. Briggs (1940) described *L. aurea* whilst Lynch (1971) examined *L. alboguttata* (as *Cyclorana alboguttatus*).

The paucity of data available regarding osteology of the Australian hylids indicates a need to establish the limits of variation within a species of those characters commonly in usage in the definition of species groups (Duellman 1970). It is also necessary to determine the validity of such character states with reference to the Australo-Papuan fauna.

For these reasons, a frog species was chosen with a known wide geographic range having evidence of isolation of populations for varying periods of time. *Litoria infrafrenata* is the largest tree frog in the world (maximum length 135 mm) so that ease of preparation of material adds to its suitability for study. Its distribution ranges throughout New Guinea and includes the north-eastern portion of the Cape York Peninsula in Australia. Two subspecies are recognised: *infrafrenata infrafrenata* found in Cape York and throughout New Guinea, and *infrafrenata militaria* restricted to New Britain (Tyler 1968). The subspecies are delineated by presence or absence of a projecting pollex. The karyotype of *L. infrafrenata* appears to differ in basic chromosome number from all other Australo-Papuan hylids so far examined (Menzies and Tippett 1976). This species, then is of particular interest in the general evolution of Australo-Papuan hylid fauna and an analysis of skull and skeletal characters is relevant to this overall study.

## MATERIAL AND METHODS

*L. infrafrenata militaria* from Keravat, New Britain. South Australian Museum (SAM) R7030, R7031, R7032, R7037, R7153, R7155.

*L. infrafrenata infrafrenata* from Aitape, New Guinea. SAM R4156, R4157, R4159, R4160, R4161, R4162.

*L. infrafrenata infrafrenata* from Tully, N. Queensland.

Six specimens obtained live from banana inspection depot of S.A. Department of Agriculture 1975-1976. SAM R15854, R15855, R15856A, R15856B, R15857.

[1] The identification of this animal is suspect as the locality is given as Cape York Peninsula; the species is not known to occur as far north.

Animals were sexed and morphological measurements were made before preparation of the skulls. Dry preparations of the skulls were made with the exception of one entire skeleton from Tully which was prepared as an alizarin.

The following measurements were made of the skulls using dial calipers: skull length (the absolute length of the skull), skull width, skull depth, the depth of pars dentalis of premaxillary, height of alary processes of premaxillary, length of anterior ramus of squamosal, length of posterior ramus of squamosal, distance from tip of anterior ramus of squamosal to post orbital process of pars facialis of maxillary (Table 1).

TABLE 1 MEASUREMENTS OF SKULLS OF *LITORIA INFRAFRENATA INFRAFRENATA* FROM TULLY, QLD. (AUSTRALIA) AND AITAPE (NEW GUINEA), AND *LITORIA INFRAFRENATA MILITARIA* FROM KERAVAT, NEW BRITAIN.

| Locality | | Depth of skull as a percentage of length | Breadth of skull as a percentage of length | Per cent distance to maxillary spanned by zygomatic arm of squamosal | Height of alary processes in relation to pars dentalis |
|---|---|---|---|---|---|
| Tully, Qld. (2♀♀, 3♂♂) | Mean | 42 | 107·4 | 53·8 | 2·98 |
| | Standard deviation | 1·58 | 8·23 | 7·82 | 0·4 |
| | Range | 41-44 | 100-114 | 41-61 | 2·35-3·82 |
| Aitape, New Guinea (1♀, 5♂♂) | Mean | 41·67 | 107 | 51·33 | 2·74 |
| | Standard deviation | 2·34 | 10·78 | 6·53 | 0·25 |
| | Range | 39-45 | 91-122 | 39-57 | 2·31-3·04 |
| Keravat, New Britain (3♀♀, 3♂♂) | Mean | 46·33 | 117·8 | 74 | 2·61 |
| | Standard deviation | 3·2 | 5·2 | 2·28 | 0·18 |
| | Range | 42-50 | 114-125 | 72·78 | 2·47-2·84 |

Outline drawings of selected skulls were made using a Wild M5 stereoscopic microscope with a Wild camera lucida attached.

## OBSERVATIONS

*Generalised description of the skull of L. infrafrenata infrafrenata.*

The specimen used for this description was a female: SAM R15857 of S-V 91·1 mm from Tully, Qld., Australia (Fig. 1).

The skull is generally broader than long with a snout in both profile and dorsal view that is rounded. The dorsal surfaces of the skull are smooth and unornamented and the skin overlying the head is freely movable. There is no evidence of prenasal, internasal or dermal sphenethmoid bones. Similarly there are no labial flanges nor occipital crests present. The anterior supraorbital margins of the frontoparietals are expanded in the form of a flange. Posterolaterally, the frontoparietals do not overlap the crista parotica. The anterior arm of the squamosal extends approximately half the distance to the maxillary. The posterior arm of the squamosal is slightly shorter than the anterior arm, expanded medially and overlaps and broadly articulates with the distal portion of the crista parotica.

The pterygoid is only moderately robust. The medial ramus is well developed and makes a bony articulation with the otic capsule. The anterior ramus has an extensive articulation with the maxillary at approximately mid-orbit, whilst the posterior ramus is poorly ossified and articulates with the ventral arm of the squamosal. The prootics and exoccipitals are fused and the columella is bony. The quadratojugal is well developed; it articulates anteriorly with the maxilla and posteriorly with the ventral arm of the squamosal. The parasphenoid lacks odontoid structures and extends anteriorly to the level of the widest portion of the supraorbital frontoparietal flange.

The premaxillaries are narrow and separated medially by connective tissue. The alary processes are widely separated medially and are posteriorly inclined at slightly less than an 80° angle. The processes are perpendicular to the pars dentalis and approximately four times as long as the depth of the pars dentalis. The premaxillaries articulate laterally with the pars palatina and pars dentalis of the maxillary; small palatine processes are present posteromedially on the premaxillaries.

The prevomers do not converge medially, the anterior borders lying posterior to the premaxillary dentigerous processes. Posterolaterally the prevomers bear wings forming the anterior, medial and posterior margins of the choanae. The dentigerous processes are small and moderately separated; they lie perpendicular to the midline and bear 9-11 teeth.

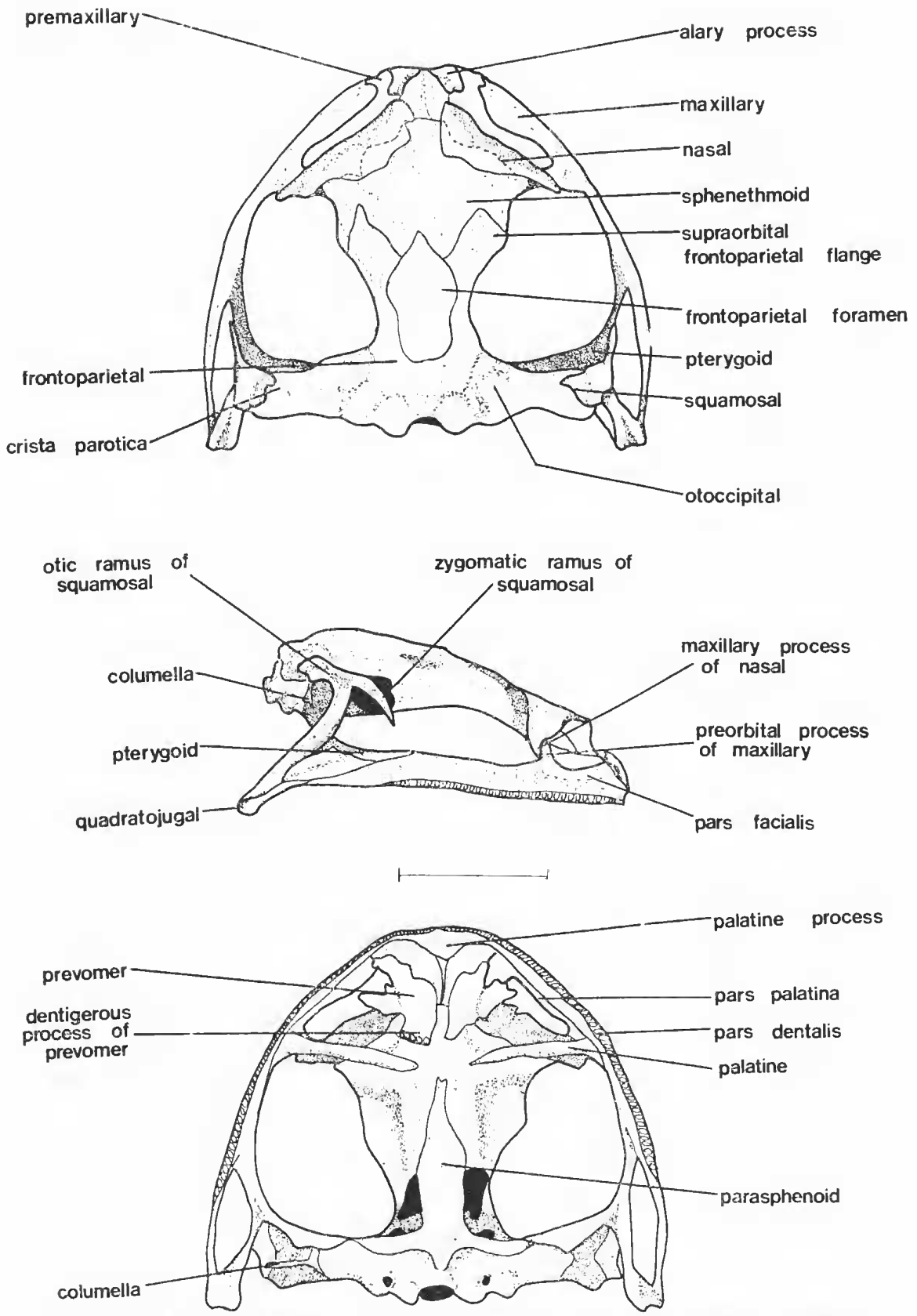



FIG. 1. Dorsal, lateral and ventral views of skull of *Litoria infrafrenata infrafrenata* R15857, ♀ from Tully, Qld. The scale represents 10 mm.

The palatines are narrow, slender bones forming the posterior margins of the choanae, with the distal ends slightly expanded and lying adjacent to the maxillaries; the posterior ends lie on the anterior ventrolateral corners of the sphenethmoid. The palatines bear very small posteroventral shelves.

The nasals are narrow and poorly ossified; the anterior tips are extended to meet the internasal septum at the level of the tips of the alary processes of the premaxillaries. The nasals are barely separated from one another medially and overlap the sphenethmoid in places. The maxillary process of the nasal is sharp and slender and articulates with the posterior process of the pars facialis; it does not extend to the level of the maxillary.

The maxillary bears a well developed pars facialis anterior to the orbit with all the surfaces free; the pars palatina is minute, extending the length of the maxillary ventromedially to the pars dentalis; the maxillary articulates with the slender quadratojugal firmly at the level of the prootic foramen.

The sphenethmoid is well ossified with the nasals extending anteriorly beyond its anterior terminus.

The frontoparietal fontanelle is moderately sized and extends approximately half the length of the orbit. The frontoparietals are moderately developed, the anterior margin is almost indistinguishable anteriorly in the area of overlap of the frontoparietal and sphenethmoid, both bones forming there a slightly upturned supraorbital flange terminating at the posterior margin of the orbit. The frontoparietals have smooth distal margins which do not extend posterolaterally over the crista parotica.

### *Variation*

The descriptive format of variation of individual bones employed here follows that of Trueb (1973).

*Frontoparietals:* The frontoparietals are paired elements which may or may not be separated from the prootic and exoccipitals by connective tissue. (The presence of connective tissue is the usual condition in the hylids.) Variation can occur in the extent to which the frontoparietals fuse with each other and with the surrounding elements (exoccipital, prootic, sphenethmoid and nasals). Further variation occurs in the extent to which these bones are ossified. Ossification of the frontoparietals is generally an indication of the overall ossification of the skull.

In *L. infrafrenata infrafrenata* and *L. infrafrenata militaria* the presence of a supraorbital frontoparietal flange is consistent in all specimens examined. In the Tully and Aitape populations the frontoparietal foramen is generally broad and ovoid, whilst in the Keravat population (*L. infrafrenata militaria*) the foramen is partially covered by bone in two specimens.

In all but one (R15857) of the Tully specimens the frontoparietal gives the appearance of being a very thin bone, whilst in the Aitape population the bone appears to be thicker, and in the Keravat population the frontoparietals can be described as well ossified.

The general shape of the bones and their fusion with the surrounding elements is consistent between the three populations.

*Nasals:* The paired nasals can vary greatly in size and shape. They can fuse to form a single element and the extent of ossification is very labile. They are equally variable in the existence and extent to which they articulate with other skull elements.

The three populations show of all characters examined the greatest qualitative interpopulation variation in the relationship of the nasals to the sphenethmoid, and in the ossification of the nasals (Fig. 2).

In the Tully population, the nasals are very thin bones (in fact opaque in appearance) that articulate along their posterior edge with the anterior edge of the sphenethmoid. In all but one of the specimens examined (R15857) the sphenethmoid does not extend anteriorly between the nasals and the anterior extension is slight.

In the Aitape population, the nasals are again very thin bones, two specimens showing slight signs of some additional bone deposition along the anterior edge. The posterior margins of the nasals articulate with the sphenethmoid which extends slightly forward between the two nasal bones in these specimens.

In the Keravat population, the sphenethmoid extends between the nasals to the level of the anterior margins of these bones. The bones again are opaque but consistently show some signs of deposition of bone along the anterior margins to a greater extent than shown by Aitape specimens.

The maxillary processes of the nasals articulate with the preorbital process of the maxillary in all three groups.

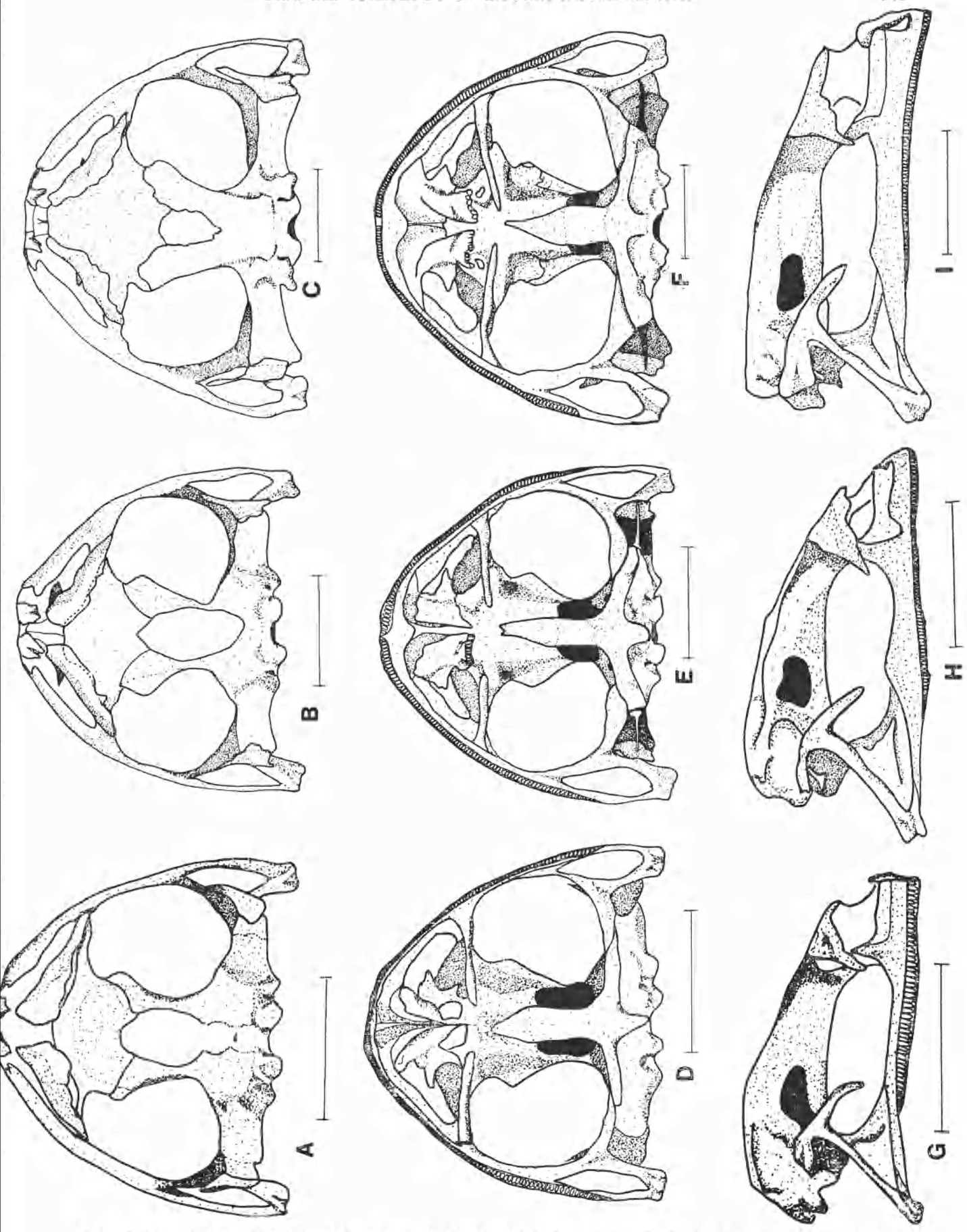



FIG. 2. Dorsal, ventral and lateral views of skulls of *Litoria infrafrenata*. A, D, G, *L. i. infrafrenata*, R15854, ♂ from Tully, Qld. B, E, H, *L. i. infrafrenata* R4157, ♂ from Aitape, New Guinea, and C, F, I, *L. i. militaria*, R7030, ♂ from Keravat, New Britain. The scale represents 10 mm. To aid comparison, diagrams have been reproduced to the same size.

*Premaxillaries*: The premaxillaries are paired dermal elements which may or may not bear teeth on the pars dentalis. The premaxillaries may be narrow or broad and the pars palatina may be extended into a broad shelf or be greatly reduced. In addition the pars palatina may be expanded at its lateral extremity or be very narrow medially. In fact according to Trueb (1973) the nature of the palatine processes is a useful specific character. These processes may or may not articulate with each other. Variation occurs, too, in the structure and orientation of the alary processes. These may be exceedingly short (less than or equal to the height of the pars dentalis) or very long (to five times the height of the pars dentalis).

The alary processes in some species are known to slope anteriorly, usually at about 80° with the horizontal plane of the skull. At the extremes, the processes may be displaced anteriorly at angles of 10° to 20°. Most alary processes, however, are nearly vertical, or inclined posteriorly at angles no greater than 135°. The alary processes generally consist of a bony shaft that is convex anteriorly (or ventrally) and concave posteriorly (or dorsally). An exception is *Plectrohyla* in which the alary processes are bifurcate.

There is little to no variation in the premaxillaries between the three populations of *L. infrafrenata*. All specimens have teeth on the pars dentalis. The premaxillaries are narrow and the pars palatina is extended into a broad shelf. The alary processes do not articulate with each other and are moderately long (2·3 to 3·0 times the length of pars dentalis). They are inclined posteriorly at an angle of 80° to the horizontal plane of the skull. The shape of the processes is in no way outstanding.

*Maxillaries*: The pars dentalis of the maxillaries may or may not bear teeth. The maxillaries bear a lingual ledge termed the pars palatina. They are further expanded dorsolaterally into a facial flange, the pars facialis, which usually has a preorbital process and, less often, a postorbital process. At the most, the pars facialis articulates at five separate points with the remainder of the skull. These are (1) the pars dentalis and pars palatina at the lateral edge of the premaxillary; (2) the preorbital process at the maxillary process of the nasal; (3) the pars dentalis and pars palatina sometimes articulate at the anterolateral edge of the anterior pterygoid ramus; (4) the postorbital process articulates with the zygomatic process of the squamosal; and (5) the posterior end of the maxillary articulates with the quadratojugal.

Variation can occur also in articulation with the squamosal, quadratojugal and nasal and in the development of the preorbital and postorbital processes of the pars facialis.

There is little to no variation in the maxillaries between the three populations of *L. infrafrenata*. A postorbital process is not present in this species, but the pars facialis articulates at the other four points. There is no variation in articulation with the maxillary process of the nasal.

*Quadratojugals*: These bones are highly variable in occurrence and are frequently lost or reduced, particularly in smaller frogs or in those in which ossification is reduced. Reduction is always in an anteroposterior sequence, the first sign of reduction being the loss of articulation with the maxillary.

The quadratojugals articulate with the maxillary in all specimens of the three populations of *L. infrafrenata* examined.

*Parasphenoid*: Variation in this bone is slight and concerns the length of the cultriform process, the presence and orientation of the alae and the presence of odontoid structures ventrally.

Any variation in these features in the groups under discussion is so slight as to be unnoticeable. Odontoid structures are not present (see Fig. 2).

*Prevomers*: Trueb (1973) considers the prevomers to be amongst the most variable bones in the skull. The anterior ends of these bones usually lie in connective tissue and the lateral wings form the bony anterior, medial and posteromedial margins of the internal nares. The dentigerous processes generally lie at a level slightly anterior to the palatines. Minor variation is found in the overall size of the bones and in the orientation of the dentigerous ridges (these latter characters are useful diagnostically at genus and species levels and may be transverse, oblique, curved or angled). Teeth are sometimes absent and odontoids are occasionally present in the absence of true teeth. The prevomers have been known to fuse with palatine elements and variation also occurs in the subdivision into discrete anterior and posterior elements.

Variation between the three populations lies in the orientation of the dentigerous processes of the prevomers. The overall size and shape of the bones appears to scarcely differ between the groups and the relationship between the prevomers and the palatines is consistent within the species. In the Tully population, the dentigerous processes, when present, are transverse, as are those of the Aitape population. However, the dentigerous processes of the Keravat population are curved.

*Palatines*: These bones usually lie adjacent to the maxillaries and articulate with the sphenethmoid medially. They are always edentate and may have a ventral transverse ridge which may be smooth or serrate. The palatines are frequently reduced in length or lost, reduction being in a medial to lateral direction.

Variation in the palatines is not discernable in the specimens examined.

*Pterygoids*: This triradiate bone shows variation in the nature of the articulation of the anterior and medial rami, usually at the midlevel of the orbit. If the medial ramus is absent, or lacks a cranial articulation, or if the skull is poorly ossified, the anterior ramus usually has an extensive articulation with the maxillary.

The medial ramus may be present or absent and if present, may or may not be articulated directly with the neurocranium. The medial ramus may be reduced so that there is no bony articulation with the otic capsule, but in this case there is usually some indirect association by means of pseudobasal or basal processes.

Variation in this bone between the groups studied here is minimal. All three rami are present and a bony articulation occurs between the medial ramus and the otic capsule.

*Squamosals*: The greatest variation in this bone is in the nature and presence of the anterior (zygomatic) and posterior (otic) rami. The posterior arm can have one of three relationships with the medially adjacent crista parotica:

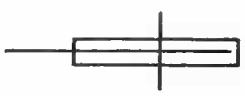
(1) bears medially expanded otic plate that broadly articulates with the dorsal portion of the crista parotica;

(2) the medial expansion of the otic ramus articulates with the posterolaterally expanded frontoparietal forming a complete or partial arch over the crista parotica; or

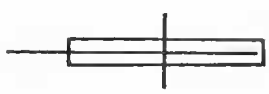
(3) the otic ramus is small and poorly developed and lies laterally adjacent to the crista parotica, but does not overlap it.

Litoria infrafrenata militaria
Keravat, New Britain

Litoria infrafrenata infrafrenata
Aitape, New Guinea



Litoria infrafrenata infrafrenata
Tully, Qld, Australia



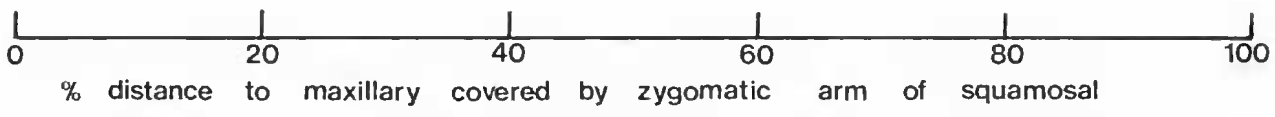



Fig. 3 Percentage distance to maxillary covered by zygomatic ramus of squamosal in three populations of *Litoria infrafrenata*. The mean is expressed by the vertical line. The rectangle represents standard deviation, and the horizontal line indicates the range.

Within the Tully population, the otic ramus varies from broad to slight overlap of the crista parotica. However, in the Aitape population, the variation is from slight overlap to no overlap at all, and in the Keravat skulls, this is again the case, with the majority of skulls showing no overlap of the otic ramus and the crista parotica.

A further variation between populations occurs in the nature of this bone and this is in the relationship of the length of the zygomatic ramus to the total distance to the maxilla. The Tully and Aitape populations would appear to have similar relationships; the anterior arm stretching from 40% to 61% of the distance to the maxilla. The anterior rami of the squamosals of the Keravat population, however, extend much further toward the maxillary; the arms covering from 72% to 78% of the distance to be spanned (Figs. 2, 3).

*Sphenethmoid*: Variation in this bone is generally a question of ossification. The anterior terminus of the bone extends to the posterior level of the nasals and posteriorly to the anterior margin of the frontoparietal fontanelle. Additional ossification can occur anteriorly in the form of an internasal septum and posteriorly around the optic foramen which is probably a feature of more heavily ossified skulls.

Variation in the shape of the sphenethmoid within the three groups under discussion has been considered in relation to the nasals. Again, in this bone there is a progression in the degree of bone deposition through the groups. The sphenethmoids of the Tully skulls are relatively thin, those of Aitape less so whilst the Keravat skulls have more extensive bone deposition.

*Otoccipital*: The prootic and the exoccipital are indistinguishably fused in modern anurans. The same kind of variation occurs in ossification as in the sphenethmoid and there can also be a reduction in the number of nerve foramina.

Little or no variation in these features is observed in the three populations.

## DISCUSSION

From the above data it is evident that in the samples studied the most noteworthy variations in the skull are:

(*a*) the extent and degree of ossification,

(*b*) the extent of development of the sphenethmoid in relation to the nasals,

(*c*) the relationship of the otic ramus of the squamosal to the crista parotica,

(*d*) the extent of development of the zygomatic ramus of the squamosal (Fig. 3), and

(*e*) the shape and nature of the dentigerous processes of the prevomers.

There does not appear to be any sexual dimorphism apart from absolute size (Table 1).

Despite its size, the skull of *L. infrafrenata* is a relatively delicate structure in contrast to the dermal coossification and exostosis found in many large South American hylids (Trueb 1970; Duellman 1970).

It could be postulated, then, that the only reasonably definitive characters distinguishing the samples are the relative length of the zygomatic ramus of the squamosal and the shape of the dentigerous processes of the prevomers. These features distinguish only the populations recognised elsewhere as subspecies (Tyler 1968).

Isolation of Australia and New Guinea occurred for the last time 6 000 years BP (Jennings 1972), so separating the frogs of the Cape York Peninsula from the population of southern New Guinea. In contrast, the isolation of the population in New Britain from New Guinea cannot be attributed to recent eustatic changes and may be a much older event.

Although New Britain and New Guinea are separated by the very narrow Vitiaz Strait, the sea floor there is 3 000 m deep. In fact the rather depauperate nature of the frog fauna of New Britain is consistent with an interpretation of the absence of a land connection with New Guinea at any time (Zweifel 1960; Tyler 1968; Brown and Tyler 1968). Therefore, the arrival of *L. infrafrenata* in New Britain is almost certainly the result of overwater dispersal. This does not imply that the greater morphological divergences between New Britain and New Guinea populations is necessarily indicative of extensive isolation. However, it is quite clear that the duration of isolation of New Britain and New Guinea is indeed much greater than that between Australia and New Guinea.

Trueb (1968) described clinal variation in the skulls of *Hyla lancasteri*. Variation between extreme populations made recognition of the one species extremely difficult. However, variation in the intermediate ranges was interpreted as suggesting uninterrupted gene flow between adjacent populations.

Variation between the three populations examined here can be described as minimal, particularly in the light of Trueb's findings. It

would seem, therefore, that the character states under consideration vary little between geographically isolated populations and can be considered as valid species indicators.

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### REFERENCES

Briggs, E. A. (1940). "Anatomy of Animal Types". Angus & Robertson: Sydney and London.

Brown, W. C. & Tyler, M. J. (1968). Frogs of the genus *Platymantis* from New Britain with description of new species. *Proc. Biol. Soc. Wash.* **81**: 69-86.

Duellman, W. E. (1970). The hylid frogs of Middle America. *Monogr. Mus. Nat. Hist. Univ. Kansas* 1: xi + 753 pp.

Gillies, C. D. & Perbody, E. F. (1917). The anatomy of *Hyla caerulea* White. 2. The skull. *Proc. Roy. Soc. Qld.* **29**: 117-122.

Jennings, J. N. (1972). Discussion on the physical environment around Torres Strait and its History. *In* D. Walker (Ed.) "Bridge and Barrier: the Natural and Cultural History of Torres Strait". Australian National University: Canberra.

Lynch, J. D. (1971). Evolutionary relationships, osteology and zoogeography of Leptodactyloid frogs. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* **53**: 1-238.

Keferstein, W. (1868). Ueber die Batrachier Australien. *Arch. Naturgesch.* **34**: 253-290.

Menzies, J. I. & Tippett, J. (1976). Chromosome numbers of Papuan hylid frogs and the karyotype of *Litoria infrafrenata* (Amphibia, Anura, Hylidae). *J. Herpet.* **10** (3): 167-173.

Parker, W. K. (1881). On the structure and development of the skull in the Batrachia Part III. *Phil. Trans. Roy. Soc. London*, **172**: 1-266.

Trueb, L. (1968). Variation in the tree frog *Hyla lancasteri*. *Copeia* (2): 285-299.

Trueb, L. (1970). Evolutionary relationships of casque-headed tree frogs with coossified skulls (family Hylidae). *Univ. Kansas Publ. Mus. Nat. Hist.* **18** (7): 547-716.

Trueb, L. (1973). Bones, Frogs and Evolution. *In* J. L. Vial (Ed.) "Evolutionary Biology of the Anurans. Contemporary Research on Major Problems". University of Missouri Press: Columbia.

Tyler, M. J. (1968). Papuan hylid frogs of the genus *Hyla*. *Zool. Verh.*, Leiden No. 96: 1-203.

Zweifel, R. G. (1960). Results of the 1958-1959 Gilliard New Britain Expedition. 3. Notes on the frogs of New Britain. *Am. Mus. Novit.* No. 2013: 1-27.